Effect of Host Plant on *Beauveria bassiana*- and *Paecilomyces fumosoroseus*-Induced Mortality of *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae)

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ABSTRACT Conidial suspensions of *Beauveria bassiana* (Balsamo) Vuillemin and *Paecilomyces fumosoroseus* (Wize) Brown & Smith were tested for pathogenicity to third-instar nymphs of *Trialeurodes vaporariorum* (Westwood) reared on cucumber and tomato plants. Nymphs were highly susceptible to infection by both fungi after a one-time application of conidia onto cucumber plants. In contrast, insects reared on tomato plants were significantly less susceptible to infection. We hypothesized that the glycoalkaloid tomatine might have been involved in antimicrobiosis on tomato leaves. Tomatine mixed with Noble agar at five concentrations was tested for its effects on germination of conidia of both fungi. Germination of conidia of *B. bassiana* was only slightly affected at the two highest concentrations of tomatine. In contrast, germination of conidia of *P. fumosoroseus* was completely inhibited at 500 and 1,000 ppm of tomatine. The in vitro tolerance of tomatine by *B. bassiana* contradicted our in vivo data. Sequestered tomatine by *T. vaporariorum* nymphs would explain, at least partially, the insect's defense against the pathogens. That little in vitro inhibition of *B. bassiana* was found supported the hypothesis that *B. bassiana* was inhibited only in vivo, after the penetration process. Inhibition of *P. fumosoroseus* might have occurred on the insect's cuticle before penetration, as evidenced by the complete inhibition of spore germination in vitro in the presence of tomatine at 500 and 1,000 ppm. An explanation for the differential in vitro sensitivity of *B. bassiana* and *P. fumosoroseus* to tomatine is being sought.

KEY WORDS *Beauveria bassiana*, *Paecilomyces fumosoroseus*, *Trialeurodes vaporariorum*, whiteflies, tritrophic level interactions, fungal entomopathogens

WHITEFLIES (HOMOPTERA: ALEYRODIDAE) are important pests of a variety of field and greenhouse crops worldwide. Because whiteflies are expected to continue to cause widespread and significant damage in many areas of the world, environmentally sound and sustainable methods of control are needed. Although most whitefly biological control research is directed toward insect parasitoids and predators (Gerling 1990, Onillon 1990), several entomopathogenic fungi have been recognized as important biological control agents of aleyrodid pests (Fransen 1990a, Lacey et al. 1996, Wraight et al. 1998). Fungi are the only entomopathogens able to invade actively through the cuticle, which is an advantage against piercing-sucking insects, and all known pathogens of Aleyrodidae are fungi. More than 20 species of fungi are reported to infect whiteflies (Fransen 1990a, Lacey et al. 1996, Steenberg and Humber 1999); and the most commonly observed fungal pathogens of whiteflies are *Paecilomyces fumosoroseus* (Wize) Brown & Smith, *Verticillium lecanii* (Zimmermann) Viégas, and *Aschersonia* spp. (Lacey et al. 1996).

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), is a serious pest to vegetables and numerous greenhouse plants, and has been reported to feed on >275 plant species throughout the world (Mound and Halsey 1978). Naturally occurring entomopathogenic fungi probably offer the greatest potential for widespread use of biological control in greenhouses (Lindquist 1996). The pathogenicities of different *Aschersonia* species and isolates have been tested on *T. vaporariorum* on cucumber, tomato, and poinsettia (references in Fransen 1990b, Meekes et al. 1996, references in Lacey et al. 1996), and many studies report on the activity of *V. lecanii* against *T. vaporariorum* in greenhouses (Hall 1982, Fransen 1990b, Ravensberg et al. 1990, Van der Schaaf et al. 1991). Less information is available about *P. fumosoroseus* and *Beauveria bassiana* (Balsamo) Vuillemin as microbial control agents of *T. vaporarorium*.

Our laboratory study evaluated host plant effects on the interaction between the entomopathogens *B. bas-*

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Table 1. Percentage mycosis (mean ± SEM) in third instars of *T. vaporariorum* inoculated with different dosages of conidia of *P. fumosoroseus* on two different host plants

Host plant	Dosage		
	33	428	1398
Cucumber	44.0 ± 5.1b	82.0 ± 9.3a	97.0 ± 1.2a
Tomato	12.0 ± 5.6b	14.8 ± 3.2ab	36.4 ± 7.1a
Chi-square (1 df)	30.52, $P < 0.001$, $n = 624$	78.05, $P < 0.001$, $n = 543$	85.19, $P < 0.001$, $n = 618$

Means for each host plant followed by the same letters are not significantly different (Tukey HSD test, $P < 0.05$). Dosages are expressed as number of viable conidia applied per square millimeter. Four to five replicates per dosage, 20–28 nymphs per replicate. The entire bioassay was repeated three times.

siana and *P. fumosoroseus* and greenhouse whitefly nymphal populations. Because preliminary tests (data not shown) showed that infection rates were significantly lower in whitefly nymphs reared on tomato than in nymphs reared on cucurbits (cantaloupe melons, pickles, and cucumbers) and because the host plant of phytophagous insects can significantly affect their susceptibility to disease (Tanada and Kaya 1993), we also evaluated the effect of tomatine, a glycoalkaloid produced by many cultivars of tomato, on in vitro spore germination of the two fungi.

Materials and Methods

Host Plants and Insect Cultures. Tomato, *Lycopersicon esculentum* Miller, 'Trust' (De Ruiter Seeds, Hybrid Seeds, Columbus, OH), and cucumber, *Cucumis sativus* L., 'Straight Eight' (Burpee, Warminster, PA), were used in the tests. We grew them in wetted peat pellets (Jiffy Products, N.B., Canada). When tomato seedlings bore two true leaves, they were replanted to floral aquapics containing a hydroponic solution (Aqua-Ponics International, Los Angeles, CA). Each rooted tomato plant was placed in a plastic petri dish (150 by 25 mm) covered with polyester organdy for ventilation. Hydroponic solution was added to the floral aquapics as required. Cucumber plants were continuously grown in peat pellets and watered as needed. The *T. vaporariorum* culture was originally started from individuals received from cultures maintained at the Department of Entomology, Cornell University (Ithaca, NY) on bean, *Phaseolus vulgaris* L.

Tomato and cucumber plants were infested with ≈50 adults of *T. vaporariorum.* Whiteflies were confined within a 4.5-cm-diameter clip cage to the underside of each test cucumber leaf or in the tissue culture dishes containing tomato plants, and were allowed to oviposit for 24 h. Adults were then removed and plants with eggs were kept in environmental chambers until the nymphs reached the third instar. Oviposition and further development of whiteflies were at 25 ± 1°C, 60 ± 5% RH, under a photoperiod 16:8 (L:D) h at 1,400–1,725 lux.

Fungi. *B. bassiana* (strain GHA, lot TGAI 97-10-1) and *P. fumosoroseus* (strain 612, lot 940917) were obtained from Mycotech, Butte, MT, as unformulated, dry conidial powders containing 1.4×10^{11} (*B. bassiana*) and 1.8×10^{11} (*P. fumosoroseus*) conidia per gram and >90% claimed viability. *Paecilomyces fumosoroseus* 612 was isolated from an infected adult *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) on a soybean leaf (Weslaco, TX, 1993). *B. bassiana* strain GHA (Bradley et al. 1999) has its origins in an infected *Diabrotica undecimpunctata undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae) in Oregon.

In Vivo Bioassay System. The fungi were assayed against early third-instar *T. vaporariorum* nymphs reared on each of the two host plants. Both fungi were assayed following the methodology described by Wraight et al. (1998). The fungi were applied to whitefly-infested leaves as 1-ml aliquots of conidial suspensions using a Potter precision spray tower (Berkard, Rickmansworth, Hertfordshire, England). Leaves were not excised for the spray applications of the fungi but were taped, ventral side up, to a sheet of rigid plastic cut to the size of the spray arena of the tower. Each suspension was sprayed at a pressure of 0.7 kg/cm^2 using the fine spray nozzle (0.25 mm orifice diameter) provided with the tower. The activity of each fungal strain on *T. vaporariorum* was assessed using three application dosages, and 20–28 nymphs per dosage. Four to five replicate tests were conducted for each dosage of each fungus. Actual dosages were determined for each fungus from blocks of 1.5% water agar placed alongside the leaves in the spray tower target arena. Four 0.05-mm^2 microscope fields (500×) were scanned on each block of agar, conidia were counted, and counts were averaged and expressed as dosages applied per square millimeter. These values were adjusted for percentage viability of the conidia, which was obtained from Sabouraud dextrose agar plus 1% yeast extract plates sprayed at the time of treatment. Adjusted dosages are given in Tables 1 and 2. Five replicated carrier (0.01% aqueous Tween 80) controls were included with each fungal treatment. The entire bioassay was repeated three times.

After spray applications, each test plant was enclosed in a plastic bag, and held for 24 h under saturated humidity conditions at 25 ± 1°C. Thereafter, plants were unbagged and the units were further incubated at 25 ± 1°C, 50% RH, and a photoperiod of 16:8 (L:D) h. Plants were watered as required. Nymphs were monitored daily for 7 d for mortality. *B. bassiana* infection was easily diagnosed by the presence of a red pigment in the hemocoel of infected whitefly nymphs that persisted until after host death (Eyal et al. 1994, Wraight et al. 1998). In situ diagnosis

Table 2. Percentage mycosis (mean ± SEM) in third instars of *T. vaporariorum* inoculated with different dosages of conidia of *B. bassiana* on two different host plants

Host plant	Dosage		
	11	432	1271
Cucumber	39.0 ± 8.3b	65.2 ± 9.7ab	95.0 ± 2.7a
Tomato	17.1 ± 5.1a	28.0 ± 5.1a	38.7 ± 14.9a
Chi-square (1 df)	13.27, $P < 0.001$, $n = 666$	27.69, $P < 0.001$, $n = 594$	70.78, $P < 0.001$, $n = 642$

Means for each host plant followed by the same letters are not significantly different (Tukey HSD test, $P < 0.05$). Dosages are expressed as number of viable conidia applied per square millimeter. Four to five replicates per dosage, 20–25 nymphs per replicate. The entire bioassay was repeated three times.

of *P. fumosoroseus* infection in whitefly nymphs is less obvious. Therefore, all dead nymphs from the *P. fumosoroseus* treatments (and the few dead nymphs from the *B. bassiana* treatments that were not pigmented) were detached from the leaf surface, surface-disinfected for 1 min in 0.03% chlorine bleach solution, rinsed twice in sterile distilled water, and finally plated on 2% water agar supplemented with 0.5% of the antibiotic agent, gentamicin sulfate. Plates were incubated for 48 h at room temperature (≈25°C) and cadavers were scored for sporulation (overt mycosis).

Spore Germination on Tomatine-Treated Agar. Tomatine (98% pure; Catalog No. T-4251) was purchased from Sigma (St. Louis, MO). The glycoalkaloid was dissolved in 60% ethanol. The ethanolic suspension was filter-sterilized using a 0.45-μm millipore filter and added to Noble agar (Difco, Detroit, MI) after cooling the medium to 45°C to final concentrations equal to 20, 50, 100, 500, and 1,000 ppm. One 10-ml aliquot of tomatine-treated or untreated Noble agar was poured in each of two petri dishes (100 by 15 mm) and allowed to dry in a laminar flow hood for 30 min to allow excess moisture to evaporate. A carrier control of solvent alone was not included in the test because preliminary germination tests on Noble agar containing 60% ethanol revealed no negative effects of the solvent on germination rates of *B. bassiana* and *P. fumosoroseus.* One 1-ml aliquot of *B. bassiana* or *P. fumosoroseus* conidial suspension (1×10^6 conidia per milliliter of sterile 0.01% aqueous Tween 80) was sprayed onto each dish using the Potter spray tower. The sprayed suspensions were allowed to dry in a laminar flow hood for 20 min. Thereafter, the treated and untreated dishes were incubated at 27°C and under saturated humidity conditions. Conidial germination was assessed 24 h after spraying using an inverted microscope (200×). Two random groups of 100 conidia per dish were examined for germ tube formation and elongation, and percentage germination was calculated. The entire bioassay was repeated three times.

Statistical Analysis. Only dead insects patently infected by the test fungi were included in the analysis. Percentages of mycosis in each of the fungus-host plant combinations were normalized through an arcsine square-root transformation of proportion mycosis to minimize correlations between the means and variances of the percentages data. The angular values of mycosis were analyzed by analysis of variance using SYSTAT statistical software version 5.2 (Wilkinson et al. 1992). Means were separated using the Tukey honestly significant difference (HSD) test ($P < 0.05$). Chi-square analysis was used for comparisons of binomial data (proportion mycosis and proportion spore germination).

Results

In Vivo Biossays. The viability of the *P. fumosoroseus* and *B. bassiana* conidia in the in vivo tests was 90.5 ± 1.5% and 93.5 ± 0.5%, respectively. After adjusting for viability, the respective means ± SEM of the high, medium, and low dosages for *P. fumosoroseus* were 1,398 ± 54, 428 ± 11, and 33 ± 13 conidia per square millimeter. For *B. bassiana,* they were 1,271 ± 108, 432 ± 28, and 11 ± 3 conidia per square millimeter.

On tomato plants, only 36.4% of third-instar nymphs died from mycosis after exposure to the high dosage of *P. fumosoroseus* (Table 1). A weak but significant dosage effect was found for *P. fumosoroseus* on tomato ($F = 4.93$; df = 2, 11; $P = 0.03$). Mycosis rates were significantly higher in nymphs treated on cucumber plants, reaching 97.0% at the high dosage (Table 1). There was a significant dosage response on cucumber ($F = 13.80$; df = 2, 12; $P = 0.001$). At any given dosage, significantly more nymphs died from *P. fumosoroseus* mycosis when reared on cucumber plants than when reared on tomato plants (Table 1).

Similar mortality trends were found in nymphs treated with *B. bassiana* (Table 2). When nymphs were reared on tomato plants, 38.7% died from mycosis at the high dosage and no dosage response was observed ($F = 1.08$; df = 2, 11; $P = 0.373$). On cucumber plants, rates of mycosis ranged from 39.0% at the low dosage to 95.0% at the high dosage, and a significant dosage effect was found ($F = 11.02$; df = 2, 12; $P = 0.002$). Comparisons of mycosis rates by chi-square tests again showed that at any given dosage of conidia significantly more nymphs died from *B. bassiana* infection if they were reared on cucumber plants than if they were reared on tomato plants (Table 2).

Spore Germination on Tomatine-Treated Agar. Spore germination on untreated Noble agar was 91.0 ± 2.6 for *B. bassiana* and 98.2 ± 0.5% for *P. fumosoroseus.* The fungal response to tomatine incorporated in Noble agar depended on the concentration of the alkaloid (Fig. 1). Conidia of *B. bassiana* and *P. fumosoroseus* incubated on medium containing 20, 50, or 100 ppm of tomatine attained >80% germination after 24 h. For

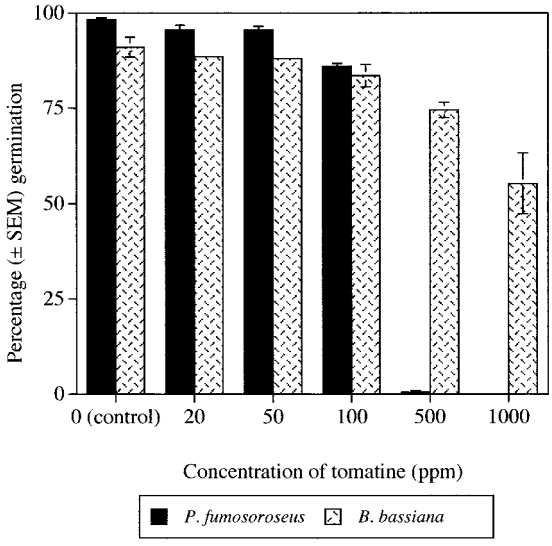

Fig. 1. Effect of a range of concentrations of the glycoalkaloid tomatine on germination of *B. bassiana* and *P. fumosoroseus* conidia on Noble agar medium at 27°C.

both fungi, there was a small but significant difference in percentage of spore germination between the control and the100 ppm concentration of tomatine ($P < 0.001$ in the two chi-square tests). A small but significant difference was also found between the control and the 20- and 50-ppm concentrations of tomatine tested against *P. fumosoroseus* ($P < 0.025$ in the two chi-square tests). Percentages of spore germination of *B. bassiana* were not different on untreated agar and agar containing 20 ppm ($P = 0.244$) or 50 ($P = 0.136$) of the alkaloid. Tomatine completely inhibited spore germination of *P. fumosoroseus* at 500 or 1,000 ppm. At these two concentrations, tomatine reduced spore germination of *B. bassiana* compared with the control germination ($P < 0.001$ in the two chi-square tests), but the inhibition (<45% at 1,000 ppm) was much less apparent than with *P. fumosoroseus* (Fig. 1).

Discussion

We have shown high susceptibility of third-instar nymphs of *T. vaporariorum* to infection by *P. fumosoroseus* and *B. bassiana* after a one-time spray application of conidia onto cucumber plants. In contrast, the same insect reared on tomato plants was significantly less susceptible to infection by the same fungal strains.

Direct comparison between previously reported findings and our findings is impossible because of different environmental conditions (laboratory versus greenhouse), fungal isolates, dosages of conidia, spray equipment, number of spray applications, and host plant cultivars. Nevertheless, our findings on cucumber agree with Fang et al. (1986) and Sterk et al. (1996), who reported good to excellent control of *T. vaporariorum* nymphs on greenhouse cucumbers with *P. fumosoroseus.* In contrast to our data on tomato, *P. fumosoroseus* was credited with excellent control of *T. vaporariorum* on greenhouse tomatoes (Bolckmans et al. 1995, Sosnowska and Piatkowski 1996, van de Veire and Degheele 1996). Differing interactions among tomato variety, pathogen strain, whitefly strain, and glycoalkaloid level may account for the differences between these previous studies and our current study. K. Bolckmans (cited in Lacey et al. 1996, p. 417) reported on the effect of host plant on activity of *P. fumosoroseus.* In greenhouses in Europe, Bolckmans found that onset of mortality and secondary spore production in *T. vaporariorum* in tomatoes treated with suspensions containing 10^6 conidia per milliliter were significantly delayed relative to treatments in cucumbers. Our data appear to concur with Bolckmans's findings. Applications of *B. bassiana* against greenhouse whitefly on cucumbers were mentioned by several authors. The fungus was effective on immature stages (Borisov and Vinokurova 1983) but was greatly dependent on high temperature and relative humidiry (Treifi 1984), conditions that favor the development of saprophytes on honeydew. We did not find reference to the use of *B. bassiana* against *T. vaporariorium* on tomatoes.

Our in vivo findings on tomato point to a potential host plant-mediated antibiosis, possibly caused by the action of tomatine, as shown for *P. fumosoroseus* and to a lesser degree for *B. bassiana* in our in vitro tests.

Tomatine, especially in its steroidal form alpha-tomatine, is well-known for its antifungal (fungitoxic or fungistatic) effects on fungal plant pathogens (Pegg and Woodward 1986, Jiratko 1993) and for its bacteriostatic activity against several bacterial plant pathogens (Roddick 1974, Kumar and Prasad 1989). Tomatine also has detrimental effects on development or performance of insect pests in several orders (Gallardo et al. 1990, Hirano et al. 1994, Sanford et al. 1996, Stamp and Osier 1998). In this regard, tomatine is a beneficial allelochemical.

However, some forms of interaction at the tritrophic level create a potential dilemma to controlling herbivorous pests through chemical antibiosis in plants. In laboratory tests, alpha-tomatine was found to be toxic to *Hyposoter exiguae* (Vier.) (Hymenoptera: Ichneumonidae), a parasitoid of *H.* zea (Campbell and Duffey 1979). The parasitoid acquired the alkaloid from its host after the host had ingested the alkaloid. Tomatine-containing prey [*Manduca sexta* (L.) (Lepidoptera: Sphingidae)] often deterred predation by *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) (Traugott and Stamp 1996), thus adversely affecting development time, mass gained, and overall performance of the predator.

The host plant of phytophagous insects can also significantly affect their susceptibility to disease, either through dietary stress or direct antimicrobial activity of the plant (Tanada and Kaya 1993). Many plants produce antimicrobial compounds, which inhibit the activity of entomopathogens. However, few studies report the effects of tomatine on entomopathogenic fungi. Gallardo et al. (1990) found that alpha-tomatine inhibited in vitro colony formation and growth of *Nomuraea rileyi* (Farlow) Samson. To-

matine was a potent inhibitor of in vitro conidial germination and mycelial growth of *P. fumosoroseus* (Lacey and Mercadier 1998) and of *B. bassiana* (Costa and Gaugler 1989). Colony formation and growth of *B. bassiana* were severely inhibited by 100 mg/liter (=100 ppm) of tomatine in unbuffered oatmeal dodine agar, suggesting that germination and growth would be inhibited when an insect, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), consumes conidia along with foliage containing 0.1 mg/g of fresh weight (=100 ppm) of this compound (Costa and Gaugler 1989).

Our finding for tomatine against *B. bassiana* disagree with Costa and Gaugler (1989) and also with our in vivo data on the effect of tomato plant on *B. bassiana*-induced mortality in *T. vaporariorum.* Variations to tolerance of pesticides in entomopathogenic fungi are well documented. Such potential differential sensitivities to tomatine and other alkaloids of different species of entomopathogenic fungal species or even of local populations of one fungal species have been suggested by Costa and Gaugler (1989). An explanation for the in vitro differential sensitivity of *B. bassiana* and *P. fumosoroseus* to tomatine is being sought.

Only Gallardo et al. (1990) reported on the in vivo effects of tomatine on the performance of an entomopathogenic fungus at the tritrophic level (although these authors used an artificial diet in their studies). Gallardo et al. (1990) found that at the LC50 of 10 conidia per square millimeter, alpha-tomatine (at 0.9 micro mol/g wet weight of diet) protected larvae of *H. zea* against *N. rileyi* and increased survivorship, whereas at the LC90 (30 conidia per square millimeter), it inhibited development of the fungus. The authors concluded that the allelochemical retained its antifungal qualities beyond the second trophic level, inhibiting the development of *N. rileyi* in *H. zea.* The findings of our in vivo study, truly conducted at the tritrophic level, concur with Gallardo et al. (1990). Ours is the first demonstration of a form of interaction at the tritrophic level host plant/hervivore/entomopathogenic fungi, in which the herbivore is a piercing-sucking insect.

We did not study the mechanisms of inhibition of *B. bassiana* and *P. fumosoroseus* on the cuticle of whiteflies reared on tomato plants. However, because fungal pathogens usually infect their hosts by penetrating the cuticle, third trophic interactions between host plants and fungal entomopathogens must occur either during cuticular penetration or after infection. There is no available information on the presence and, if present, on concentrations of tomatine in the cuticle or hemolymph of insects. However, sequestered tomatine by *T. vaporariorum* nymphs would explain, at least partially, the insect's defense against *B. bassiana* or *P. fumosoroseus.* That little in vitro inhibition of *B. bassiana* was found in our study reinforces the hypothesis that *B. bassiana* was inhibited in vivo, after the penetration process. In contrast, inhibition of *P. fumosoroseus* might have occurred on the insect's cuticle before penetration, as occurred in vitro with complete inhibition of spore germination in presence of tomatine at 500 and 1,000 ppm. Further research is definitely required to fully explain the relative tolerance of *B. bassiana* to tomatine compared with *P. fumosoroseus,* but also to fully explain the similar response of whiteflies to both fungi at the third trophic level. Finally, some other allelochemical(s) (e.g., chlorogenic acid, rutin, 2-tridecanone, catecholic phenolics) might have been involved in the inhibition of the fungi at the third trophic level. Therefore, the sensitivity of *B. bassiana* and *P. fumosoroseus* to these compounds needs to be assessed in in vitro tests.

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